Within-tree Fluctuating Asymmetry of Mountain Birch in Subarctic Sweden

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Master Thesis no. 183
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ABSTRACT

The mountain birch ecosystem forms the northern treeline in subarctic Europe. Since the treeline is extremely sensitive to temperature, stress in mountain birch can be used as an indicator of stress on the ecosystem as a whole, and in predictions of how climate change factors will influence the subalpine-tundra ecotone and treeline dynamics. Fluctuating asymmetry (FA) is a common technique for assessing stress in mountain birch. While no previous research has studied within-tree variations of FA in mountain birch, other species have shown significant variation depending on location of the leaf within the crown, and thus leaf collection location is important to consider when sampling. The objective of this study is to determine if a relationship exists between leaf FA and location within the tree crown of mountain birch leaves across three elevation zones in subarctic Sweden. Leaves were collected from various locations within the crown with regards to height (bottom, middle, top), direction (north, east, south, west), and position (inner, outer), and at 3 elevation sites (valley, forest-limit, treeline). A nested ANOVA was used to analyze the data. The treeline site showed a higher amount of FA than the valley or forest-limit sites ($P = 0.0228$), but no significant difference was found between any of the within-tree leaf locations. This suggests that there is no influence from crown location on FA in the leaves of mountain birch, and therefore future studies involving FA can freely sample leaves from any location within the crown.

Keywords: Mountain Birch, *Betula pubescens* ssp. *Czerepanovii,,* fluctuating asymmetry, treeline, subartic, developmental stability,Abisko,

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1. INTRODUCTION

The mean annual temperature has been rising globally over the last century, with the most pronounced and accelerated warming recorded at higher elevations and in the polar regions (Huntington & Weller 2005). Future climate models also predict warming to continue being greatest at high latitudes (Skre 2001). As the location of the northern treeline is mainly determined by temperature (Harsch et al. 2009), the greatest impact of climate change is expected to be seen within these ecosystems (Truong et al. 2007). Therefore, monitoring changes in the treeline can be a major indicator of global climate change (Neilson 1993; Hofgaard 1996).

Factors controlling the treeline are highly scale and location dependent, so individual and short-term responses may vary greatly from what would be predicted on a larger level (Sveinbjörnsson et al. 2002). In order to create accurate models and understand processes behind the large-scale changes, evaluation of short-term and individual responses is critical (Holtmeier & Broll 2005).

In these subarctic areas that are extremely vulnerable to climate change, knowledge of factors affecting the establishment and growth of a forest-forming species is essential (Eränen & Kozlov 2008). This study contributes to knowledge of the forest forming species mountain birch (*Betula pubescens* ssp. *czerepanovii*) by examining fluctuating asymmetry, a common indicator of stress, within the crown of trees located along three elevation zones in subarctic Sweden.

The objective of this study is to determine if a relationship exists between leaf fluctuating asymmetry and location within the tree crown of mountain birch leaves across three elevation zones in subarctic Sweden.

2. CONTEXT AND DEFINITIONS

The mountain birch ecosystem

The mountain birch forest ecosystem represents the northern tree limit for much of Europe and Russia, and forms the subalpine belt that separates the treeless tundra from the more southerly coniferous-boreal zone (Dahl 1975). Mountain birch (*Betula pubescens* ssp. *czerepanovii*) is the only forest-forming species within this subalpine zone and has the most northern range of any deciduous tree in the world (Wielgolaski 2005).

The mountain birch ecosystem belt extends from southern Greenland, across Iceland, and through northern Fennoscandia (Norway, Sweden, Finland, and the Kola Peninsula in Russia) (Wielgolaski 2001). Palynology and radiocarbon dating show birch present in Fennoscandia as early as 12,000 B.P., and historic evidence suggests that the mountain birch forest represents a relatively stable final state of vegetative development, and not just a stage of succession or a cultural product (Aas & Faarlund 2001).

Mountain birch forests in the Fennoscandia area are generally classified into six vegetational community types: crowberry birch forest (*Empetro-Betuletum pubescentis*, Nordhagen 1943), lingonberry birch forest (*Vaccinio vitis-idaeae-Betuletum*, prov.), bilberry birch forest (*Vaccinio myrtilli-Betuletum*, prov.), dwarf cornel birch forest (*Corno-Betuletum*, Aune 1973), meadow birch forest (*Geranio-Betuletum*, Nordhagen 1928, 1943 emend. Dierßen and Dierßen 1982), and cloudberry birch forest (*Rubo chamaemorei-Betuletum*, prov.) (Wehberg et al. 2005). The main determiner of forest type is soil fertility, precipitation, and temperature (Tømmervik et al. 2005). Eutrophic sites in oceanic sections are floristically most luxuriant, and oligotrophic sites in continental sections are the poorest in vascular plants and bryophytes (Väre 2001).

Betula pubescens ssp. *czerepenovii*

The taxonomy of the *Betula* genus is quite complex and controversial, largely due to the high level of hybridization between the different species (Truong et al. 2007), and the

taxonomy of the European birches has long been in dispute (Atkinson 1992). Most notably the relationship between the tree like tetraploid (2n=56) downy birch (*Betula pubescens* Ehrh), the diploid (2n=28) silver birch (*B. pendula* Roth.), and the more shrub like diploid (2n=28) dwarf birch (*B. nana* L.) (Thórsson, et al 2007). Although at one time Laestadius (1860) described 40 different birch taxa in Fennoscandia alone, only these three species are generally recognized today (Väre 2001).

The Nordic mountain birch, which is predominantly believed to be a subspecies of *B. pubescens,* varies widely in its morphology and readily hybridizes with downy birch and dwarf birch where they overlap in range (Väre 2001). Although there is evidence that the transition from downy birch to mountain birch is purely clinal, and therefore should not be considered a coherent taxon, the common trend in the nomenclature today is the name *B. pubenscens* ssp. *czerepanovii* (Orlova) Hämet-Ahti as the form found in most of Fennoscandia (Väre 2001).

The morphology and growth habit of mountain birch varies greatly, but in general it can be said to be a fairly light demanding and drought intolerant species (Atkinson 1992) that prefers a cool, humid, and maritime climate with a reliable snowpack (Hämet-Ahti 1963; Kallio & Mäkinen 1978; Kjällgren & Kullman 1998). The typical height is between 4-10 meters (Atkinson 1992), and the form varies from a single stem erect form, to multi-stem with more shrub-like characteristics (Kjällgren & Kullman 1998). Sexual reproduction is episodic, and rare at higher elevations due to low production of viable seed and poor seedling survival (Kullman 1984). Vegetative sprouting is the most common form of reproduction in poor environments, and is possibly the only type of reproduction found along the treeline (Karlsson et al. 2005). Leaves of *B. pubescens* are morphologically described as being cordate with dentate margins (Walters 1964); however, leaf size has been shown to vary significantly among trees (Senn 1992).

Stresses on mountain birch

Growing in an extreme environment, mountain birch is exposed to many biotic and abiotic stresses. One of the main hazards to the mountain birch is herbivory, in the form of

reindeer browsing and defoliation by caterpillars (Tenow 1996). Reindeer have been semi-domesticated by the Sámi people for many thousands of years, and every year they migrate through the subalpine mountain zone, feeding on birch as their preferred food source (Aikio & Müller-Wille 2005). Browsing from reindeer causes reduced growth and the formation of multiple raments; however, this rarely causes the tree to die (Helle 2001).

Insect defoliations are one of the most important disturbances in the dynamics of mountain birch forests (Neuvonen et al. 2001). Periodic outbreaks of the autumnal moth (*Epirrita autumnata*) and the less coincidental winter moth (*Operophtera brumata*) cause severe damage to the mountain birch forest (Tenow et al. 2005). The moths can cause complete defoliation and, with repeated attacks, mortality to the trees (Tenow et al. 2000). Another biotic threat is the birch rust (*Melampsoridium betulinum*), which in severe outbreaks can cause reduction in photosynthesis and early abscission (Lappalainen et al. 1995).

Although the mountain birch is adapted to harsh environments and a short growing season, shifts in weather in the subarctic may be rapid and radical in all seasons (Tenow 1996). Extremely cold late spring temperatures can kill buds that have already begun to deharden (Tenow et al. 1992). The snow depth has an impact on birch survival as well, and years with little snowpack accumulation subject the trees to exposure to wind and cold temperatures and can kill the tree, even in a dormant state (Bogaert et al. 2011).

Mountain birch and climate change

The sensitive position of the treeline environment is a balance between the treeless tundra and the boreal forest. Most of the species here are living at the very limit of their range. This balance makes the mountain birch treeline extremely sensitive to slight changes in the climate (Hasch et al. 2009). The ecosystem is also structurally simple with low productivity, making it less resilient and highly susceptible to disturbance (Sonesson et al. 200).

Many of the plant species located in these arctic environments are extremely reliant on small, protected micro-climates for their survival (Carlsson & Callaghan 1991). For

example small depressions in the land, or shelter around rocky outcrops where a deeper snowpack can form, will provide the shelter needed for many species that would not otherwise survive. Glacial till and peat create a wide range of soil types and depths, even over a relatively small area (Karlén 1973). These microclimates determine the species composition, and are necessary for individual survival (Carlsson & Callaghan 1991).

It is predicted that it is these sensitive subarctic ecosystems that will suffer the greatest effects from global climate change (Harsch et al. 2009). Small degrees of temperature differences define the varied community composition in these extreme environments (Truong et al. 2007). Climate change can also cause increases in pest/pathogen outbreaks which can further weaken an already stressed system (Walther et al. 2002). Slight changes in the little precipitation that is received can create a drought environment and reduce snowpack protection from harsh winter conditions (Dalen & Hofgaard 2005).

It has been shown that summer temperatures are the main determinant of the arctic treeline, and changes to these summer temperatures could greatly affect the position and composition of the treeline (Tranquillini 1979). As mountain birch forms the treeline, is the dominant tree species, and is essential for the survival of the mountain birch ecosystem, its response and reaction to climate change will be a determining factor in the future of these subalpine ecotones (Truong et al. 2007).

Fluctuating asymmetry

Fluctuating asymmetry (FA), or random, non-directional deviations from anticipated perfect bilateral or radial symmetry, is often used as an indicator of stress in many different organisms (VanValen 1962; Palmer & Strobeck 1986; Parsons 1990). During cellular development, factors that interfere with normal developmental processes (developmental noise) are minimized by a suite of processes known as developmental "buffers." This ability to buffer the development process from noise, and continue to develop along a predetermined path, is called developmental stability. Developmental instability (stress) occurs when noise in not properly buffered (Palmer 1994). Fluctuating

asymmetry is a result of this inability to maintain developmental stability (Parsons 1990). Since one set of genes controls for both sides of a character trait, under normal development, the two sides are symmetrical (Mather 1953). But when developmental noise is greater than an organism's ability of buffer, errors occur and the result is random deviations from symmetry (Palmer 1994).

Since it can be difficult to judge the level of stress an organism is under and often our assumptions of what constitutes as stress is not always accurate, FA can be a useful indicator in evaluating the actual stress experienced by an individual or a population (Freeman et al. 1996). Asymmetry is a particularly useful measure of developmental stability because for bilaterally or radially symmetrical traits the optimal phenotype is known (Møller 1999). By simply measuring each side of an ideally symmetrical character trait, an indication of stress at the cellular level can be obtained (Parsons 1990). In the field of ecology most indicators are lagging indicators of stress, but developmental instability is a leading indicator and can identify a problem before it reaches the point of apparent demographic consequences (Freeman et al. 1996).

There are instances in nature, however, when symmetry is not the desired outcome. Fluctuating asymmetry, which is random and caused by developmental noise, is just one type of asymmetry that can be found. In FA the difference between the right (*R*) and the left (*L*) sides of the measured trait (*R*-*L*) has a mean of zero and a normal distribution (Palmer 1996). The other two types of asymmetry that can occur are directional asymmetry and anti-symmetry, and both can happen during normal development (Graham et al. 2003a).

Directional asymmetry occurs when one side of a character trait is always larger than the other, and the side that is larger is consistent. An example of this is the human heart, where the left side is always bigger than the right. In the case of directional asymmetry the mean of *R*-*L* departs from zero, but the distribution is normal (Palmer 1994).

Anti-symmetry occurs when one side of a character trait is always larger than the other; however, it is not predictable which side will be larger. This is the case for fiddler crabs, in which either the left or right claw is larger than the other. Anti-symmetry has a

platykurtosis or bimodal distribution with a mean centered around zero (VanValen 1962). It is generally thought that, unlike FA, these types of asymmetry are genetically determined and are not indicators of developmental stability (Parsons 1990).

Fluctuating asymmetry and stress

The implications of FA as a tool for measuring developmental stability began in the1950's with the pioneering work of Mathers (1953), Thoday (1958), and others (see Graham et al. 2003a for a complete overview). Since then, FA has been widely adapted into many fields of natural science. FA has been used to study a variety of traits, from wing length in honeybees (Brückner 1976) and ridge counts in human fingerprints (Martin et al. 1982), to fossilized horse teeth (VanValen 1962) and branching in algae (Tracy et al. 1995).

FA is commonly used to measure stress in plants, both in controlled greenhouse studies and field ecology studies (Møller 1999). Plants lend themselves well to FA analysis, as they have many symmetrical structures that are easy to collect or measure in the field (Freeman et al. 1993). The FA method is inexpensive, requires little equipment, and can detect a large range of stresses (Møller & Pomiankowski 1993). It is also unique as it can look at stress in an individual plant, the population as a whole, or the entire ecosystem (Freeman et al. 1996). And since plants grow as modules it is also possible to examine within-plant variation (Freeman et al. 1993). Some previous plant studies have found FA to be a useful tool to monitor effects from herbivory (Zvereva et al. 1997), light (Roy & Stanton 1999), CO_2 concentration (Cornelissen et al. 2004), inbreeding (Sherry & Lord 1996), parasitism (Shykoff & Kaltz 1998), slope aspect (Alados et al. 2001), drought (Hódar 2002), nutrients (Otronen & Rosenlund 2001; Møller 1995), soil quality (Huether 1968), radiation (Møller 1998), salinity (Anne et al. 1998), temperature (Griffing & Langridge 1963), and competition (Rettig et al. 1997).

Within the past few years multiple studies have used FA to monitor stress in mountain birch. FA in mountain birch has been found to increase in the presence of hybridization (Wilsey et al. 1998), pollution (Kozlov et al. 1996; Eränen et al. 2009),

herbivory (Martel et al. 1999), elevation (Wilsey et al. 1998; Hagen et al. 2008), moisture (Martel et al. 1999), and temperature (Valkama & Kozlov 2001).

Despite the overall acceptance of FA as a way to monitor stress in plants, it is still poorly understood (Wilsey & Saloniemi 1999) and it has evoked some skepticism. Swaddle et al. (1994) argue that the relatively small measurement values needed in most research for FA require high levels of precision, and measurement errors are often much greater than the variation caused by fluctuating asymmetry. Kozlov (2003) demonstrates that the types of analysis used can greatly affect the outcome, and that these tests are not always formed in the appropriate manner. A number of authors have also found a difference in asymmetry between floral verses foliar parts in plants, and have found the floral parts to generally be more stable (Jennions 1996; Evans & Marshall 1996; Paxman 1956; and Sakai & Shimamoto 1965). There is much debate as well over the genetic bases of directional asymmetry and anti-symmetry, and whether they should be included in studies of developmental stability; and many articles have been written recently which support including all types of asymmetry in measurements of stress in plants (Graham et al. 1993; 1998; 2003b; Kozlov 2003; Palmer 1996).

3. METHODS

Study area

This study was carried out near Abisko, northern Sweden (68°36'N 18°77'E). The Abisko valley is situated approximately 200 km north of the Arctic Circle, on the southern shore of Lake Torneträsk, in the Scandes mountain range. The mountains here are topographically and geologically very heterogeneous (Sonesson et al. 1980).

When deglaciation occurred more than 9000 years ago (Sonesson 1974) dead-ice created a hummocky landscape, with many kettle and moraine features. The soils are predominantly glacial till, with peat occurring in local depressions (Berglund et al. 1996).

The north-south extension of the mountains to the west creates a pronounced rain-shadow effect on the Abisko valley (Bigler et al. 2006). The mean annual precipitation in the valley is only around 300 mm, while areas to the west receive as much as 1000 mm a year. The temperature ranges from a mean of +11° C in July, to a mean of -12° C in January (Abisko Research Station, unpubl.).

Due to the presence of the Abisko Research Station, the Abisko area has an exceptionally long record of climatic data available. Through this, it has been shown that the mean annual temperature has increase by 2.5° C between the years 1913 and 2006. The average annual temperature has now crossed the critical 0° mean to an annual mean of +0.6° C at some elevations, which has many cryospheric and ecological impacts (Callaghan et al. 2010).

The Lake Torneträsk region falls within the tundra-subalpine ecotone, and approximately 60% of the area is below the treeline (Sonesson et al. 1980) which forms between 600-700 m a.s.l. The vegetation is mosaic, with patches of birch forest, alpine heath, and oligotrophic mires. The majority the forests here are of the Crowberry Birch Forest (*Empetro-Betuletum pubescentis*, Nordhagen 1943) type, populated by shrubs (*Empetrum hermaphroditum* Hagerup and *Vaccinium myrtillus* L.), grasses (*Deschampsia*

flexuosa (L.) Trin.), mosses (*Pleurozum schreberi* (Brid.) Mitt., *Dicranum majus* coll, *Polytrichum* spp.), and lichens (*Nephroma arcticum* (L.) Forss., *Cladonia rangiferina* (L.) Web., *C. sylvatica* (L.) Rab.) (Sonesson et al 1980).

The birch forest is formed by the Nordic mountain birch (today most often called *Betula pubescens* ssp. *czerepanovii* (Orlova) Hämet-Ahti, but also known as *B. pubescens* ssp. *tortuosa* Ledeb. (Sonesson et al. 2001)). Most of the birch have a krummholz formation with multiple ramets, but monocormous (single-stem) trees can be found on more favorable sites (Verwijst 1988). The birch in the Torneträsk area form an open canopy, and reach a maximum height of 5-8 m, although individuals located near the treeline rarely grow above 2 m (Sveinbjörnsson et al. 1992). Due to a severe outbreak of the autumnal moth in 1955 which killed 90% of the stems, the current population of stems are predominantly the same age (Tenow 1996).

Site description

For this study birch trees were sampled from 3 different evaluation zones: valley, forest-limit, and treeline (Fig. 1). These site selections were adapted from previous studies by Sveinbjörnsson et al. (1992 and 1996). Topographical maps were used to verify elevation (Älvsby-Tryck, AB).

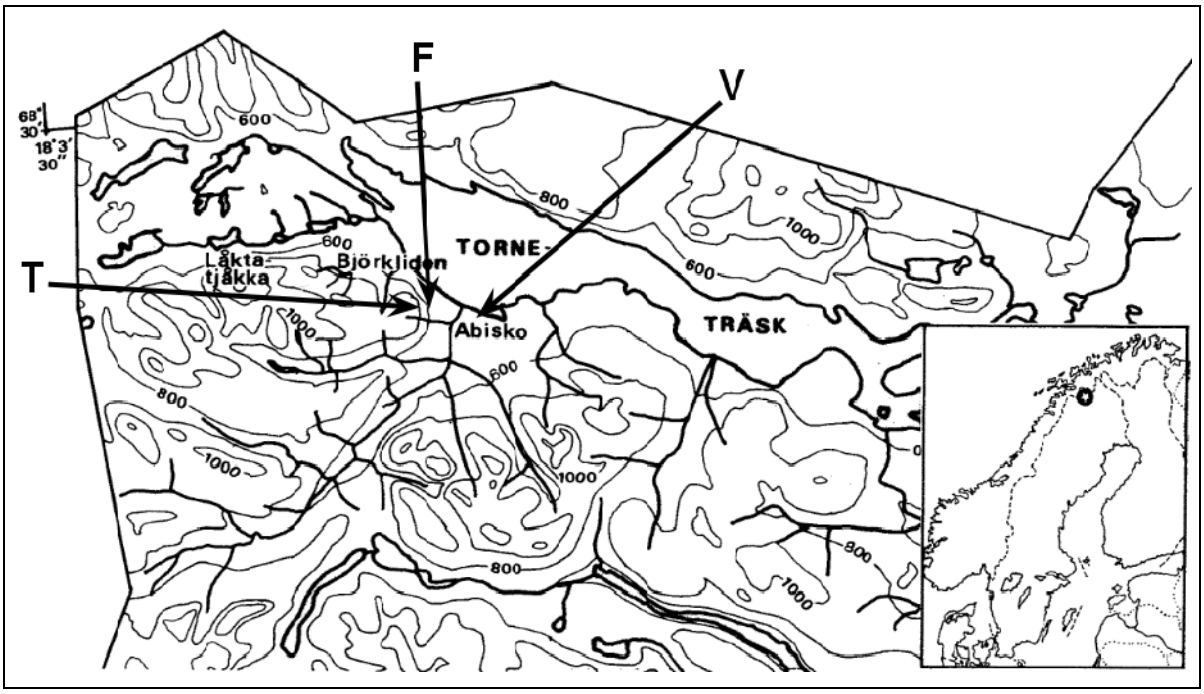

Fig. 1. Location of study sites (map adapted from Åkerman and Malmström 1986). Valley site = V, forest-limit = F, and treeline = T.

The valley site was located just north of the Abisko Research Station, within the station's 46-hector nature reserve. The valley site was approximately 150 m from the shore of Lake Torneträsk, at an elevation of 350-360 m a.s.l. The area was generally flat, although strewn with large boulders, and had a relatively homogeneous tree density.

The forest-limit site was located on the southeast slope of Mt Slåttatjåkka near Mt Njulla, at an elevation of 640-660 m a.s.l. The trees here were at a similar density to the valley site, and formed the upper limit to the continuous forest below.

The forest creates a fairly well defined border around 680 m a.s.l., and above this is the kampfzone, with birch trees existing as scattered individuals or in small clumps. The trees here were noticeably smaller in stature, and often twisted or bent. In this zone, directly above the forest-limit site, the treeline site was located (700-720 m a.s.l.).

Due to the variation in tree density and land topography in each site, measured plots were not established, but sampling was replicated laterally across each site. As the nature of this study was not to evaluate stress in the population as a whole, but rather to look at individual within-tree variation, care was taken to select trees that were representative of the area, without visible influences from micro-climate variation (e.g. a large boulder restricting growth on one side). Ten trees were sampled within each elevation zone site.

Leaf collection

Birch produce two types of shoots: long shoots (auxiblasts) and short shoots (brachiblasts) (Kozlov et al. 1996). Short shoots flush early in the growing season and develop with resources from the previous year. This is often the only type of shoot present at high elevations (Lempa et al. 2000). Long shoots emerge from the short shoots, and grow with resources obtained during the current year (Kozlowski and Clausen 1966). To insure that all sample leaves had developed during the same period, only leaves from short shoots were collected.

All sample leaves were collected between 8 and 20 of August, 2010. All samples were collected by the same individual (K.S.), and the trees were short enough to allow collection by hand.

On each of the ten trees selected from each site, 24 leaves were collected. Leaves were collected based on relative location within the crown of the tree. Three location variables were established: Height (Bottom, Middle, Top); Direction (North, East, South, West); and Position (Outer, Inner) (Fig. 2).

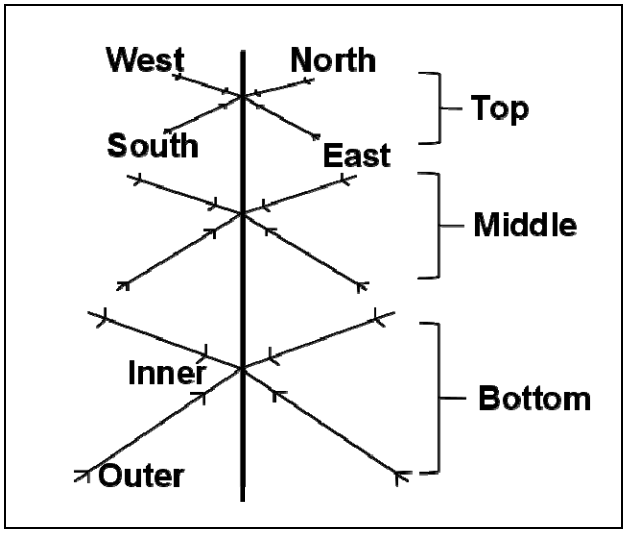

Fig. 2. Schematic diagram of leaf collection locations within the crown of an individual tree

Height treatments were selected by sampling the second branch from the bottom (Bottom), the second branch from the top (Top), and visually estimating the middle section of the crown (Middle). A compass was used to select the branches within each height zone that most closely faced the cardinal directions (North, East, South, West). Within each of these branches the second leaf from the tip (Outer), and the second leaf from the base of the branch (Inner) was collected. This created 24 location combinations within each tree. One leaf was collected from each location, on each of the 10 trees, within each elevation zone (720 leaves total).

If a leaf was damaged to the extent that measurement would not be possible, it was rejected and the next closest leaf to the location was selected. Each leaf was given a specific location code and was pressed in the field between filter paper. The dried leaves were mounted on sheets of paper and scanned into a computer as image files for measurement.

Measurement

Digital measurements (to the nearest 0.1 mm) using ImageJ 1.45 were taken of the scanned leaf images at 400% of original size. All measurements were performed by the same individual (K.S.).

For each leaf, the length was measured along the midrib from the base of the blade to the apex, and the half-way point was noted. The left (*L*) and right (*R*) widths were measured using the angle finder tool to create a 90-degree angle from the midrib. The distance from the midrib to the leaf margin was measured on the left and the right sides at the mid-point of the blade length (Fig. 3).

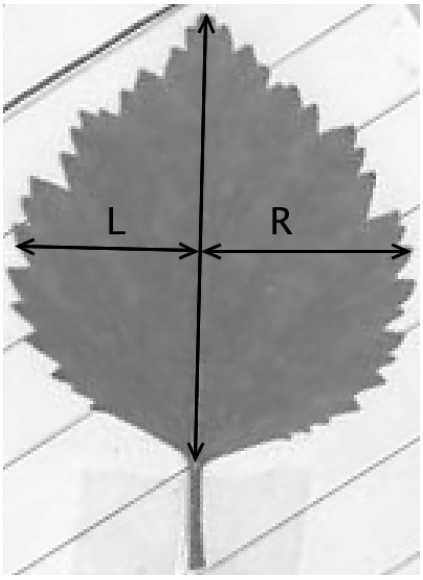

Fig. 3. Scanned *Betula pudescens* ssp. *czerepanovii* leaf showing left width (*L*) and right width (*R*).

To check the reliability of the measurements, leaves from one tree in each elevation zone (n=72) were remeasured 2 weeks after the original measurement date, without reference to prior measurement. The images from this same subset of leaves were then digitally flipped horizontally (mirror image) and measured a third time, to check for any directional bias measurement errors. The signed difference between the right and the left

side (*L*-*R*) was compared among the three measurements (original, remeasure, and mirror) with a paired t-test. For all of the paired t-test combinations (remeasure vs. original (P = 0.4328), mirror vs. original (P = 0.6118), mirror vs. remeasure (P = 0.1707)) the results were not significant. This suggests that measurement error is trivial, and can be ignored for the purpose of this study.

Data Analysis

Since leaves grow under the active tissue model, which generates multiplicative errors, the data must be log transformed before statistical analysis of fluctuating asymmetry can be performed (Cowart & Graham 1999; Graham et al. 2003b). Log transformation also corrects possible size-scaling (the variance of |*L*-*R*| increasing with increasing leaf size) that can be problematic (Graham et al. 1998). Even though measurement errors appear to be insignificant in this study, small measurement errors are normally distributed, and when superimposed on the lognormal leaf growth values, can create a mixed distribution (Graham et al. 2003b). However, averaging the replicates will diminish measurement error by a predictable amount:

$$\left[\frac{\sigma^2 - \left(\frac{\sigma^2}{n}\right)}{\sigma^2}\right] 100$$

where σ2 is the measurement error and n is the number of replicates (Wilsey et al. 1998; Graham et al. 2003). By averaging the 10 replicates for each leaf location in this study, the measurement error will decrease by 90%.

After log transformation, the data were normally distributed. A Shapiro-Wilk test showed that the data are from the normal distribution (P = 0.6899).

4. RESULTS

A nested ANOVA with the effects position within direction, direction within height, and height within site was performed on the log-transformed FA data (|*L*-*R*|), followed by a Tukey's multiple range test. The following table (Table 1.) shows the results of the nested ANOVA among the treatments.

Table 1. Results of ANOVAs of leaf fluctuating asymmetry (FA) among elevation site and within-tree leaf position for *B. pubescens* spp. *czerepanovii* growing at the northern distribution limit.

Source of variation	d.f.	S.S.	*F*	*P*
Site	2	0.00134985	4.2057	0.0228*
Height(Site)	6	0.00105471	1.0954	0.3839
Direction(Height[Site])	27	0.00401388	0.9264	0.5766
Position(Direction[Height{Site}])	36	0.00577727	0.6611	0.7392

A significant difference was found between the elevation sites, but no significant difference was found among the within-tree leaf locations. A Tukey HSD connected letters report showed that the treeline site is significantly different ($P < 0.05$) than the valley and forest-limit sites. The following figures show the means for each variable with the *P* value from a single level analysis.

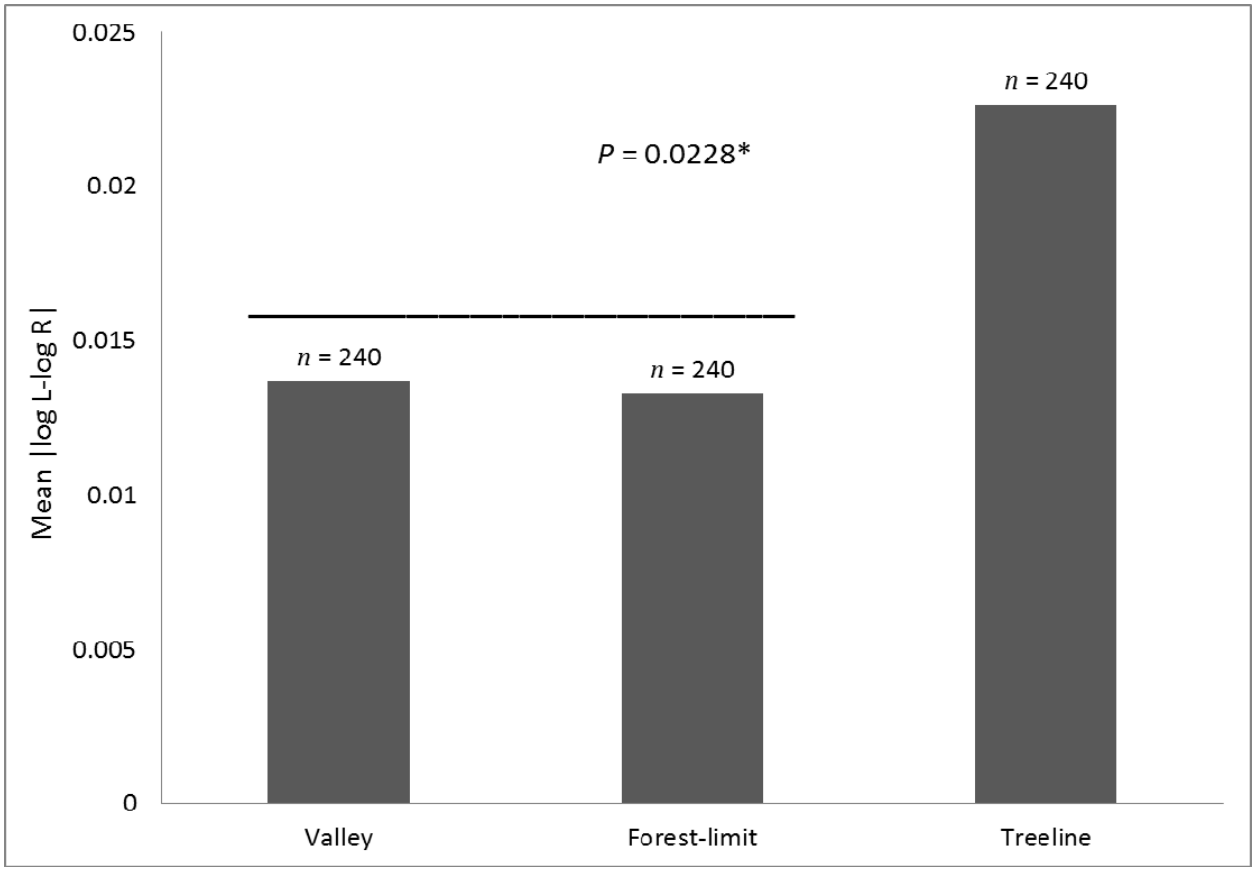

Fig. 4. Leaf fluctuating asymmetry (FA) at three different elevation sites for *B*. *pubescens* spp. *czerepanovii* growing at the northern distribution limit.

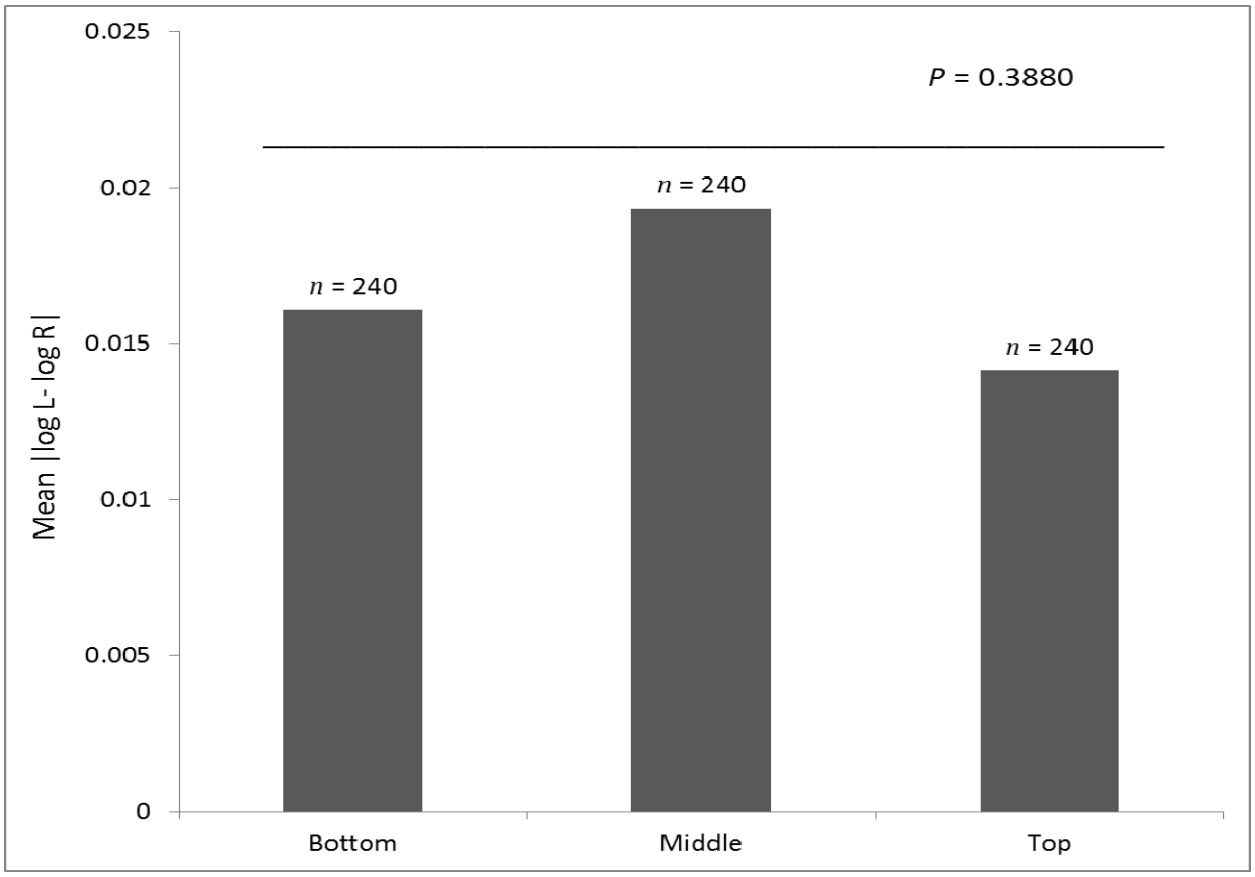

Fig. 5. Within- tree leaf fluctuating asymmetry (FA) with respect to height within the crown for *B. pubescens* spp. *czerepanovii* growing at the northern distribution limit.

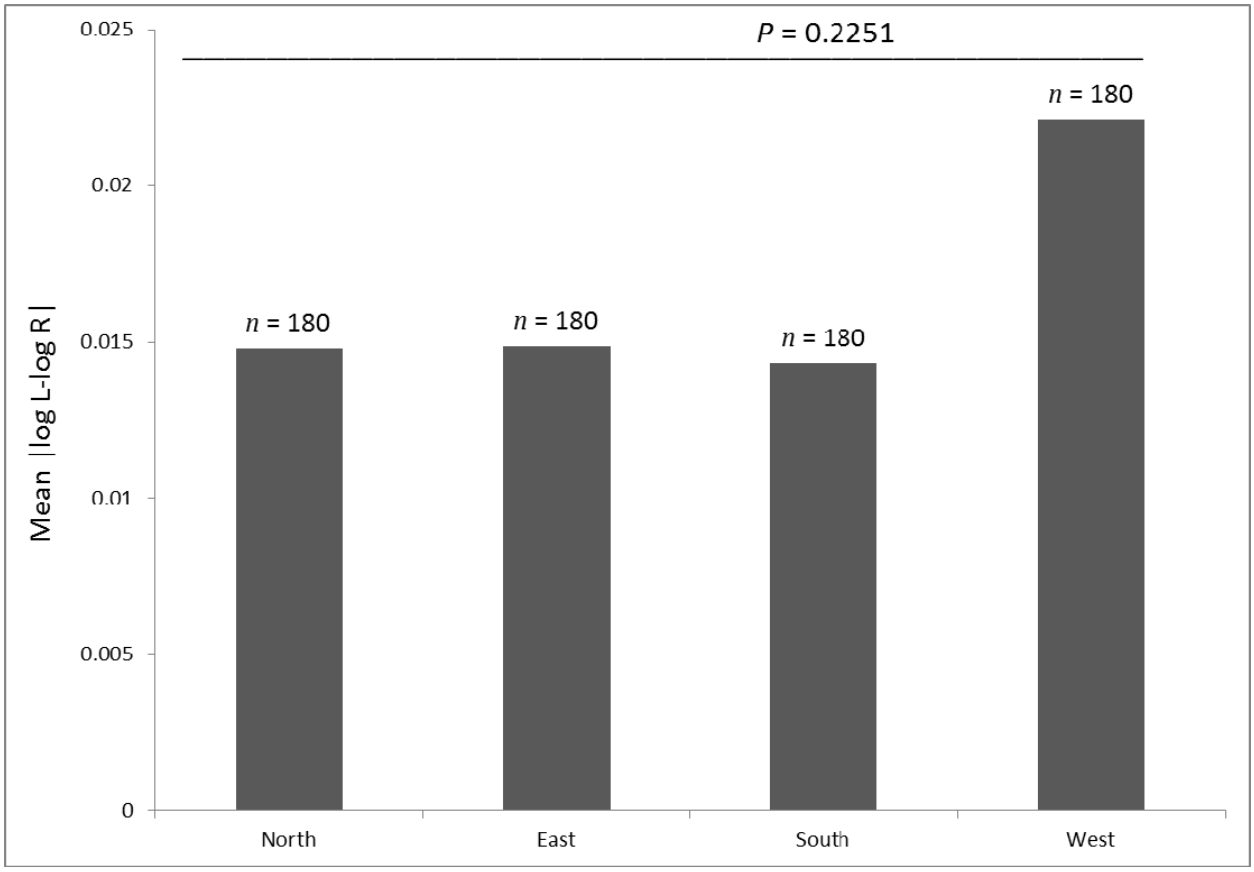

Fig. 6. Within- tree leaf fluctuating asymmetry (FA) with respect to direction within the crown for *B. pubescens* spp*. czerepanovii* growing at the northern distribution limit.

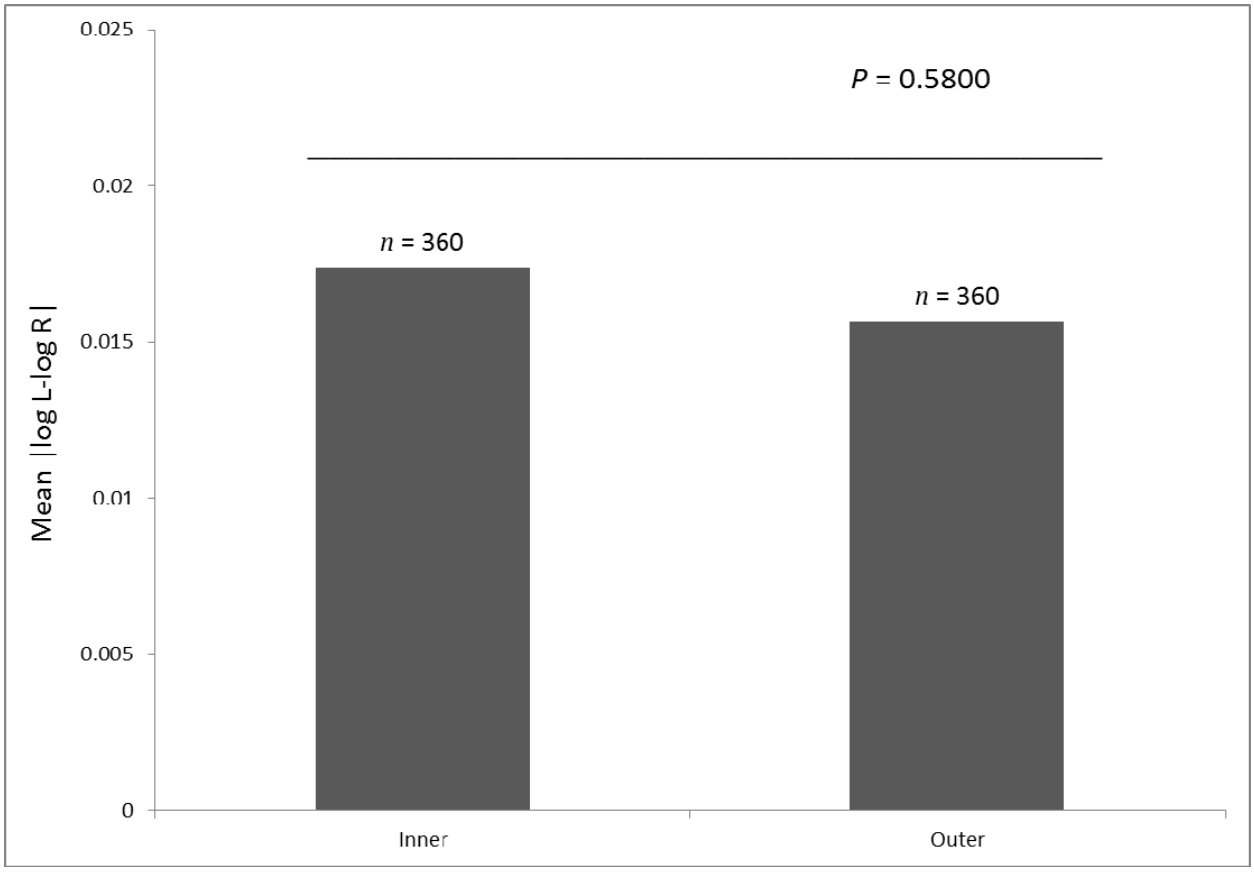

Fig. 7. Within- tree leaf fluctuating asymmetry (FA) with respect to position within the crown for *B. pubescens* spp*. czerepanovii* growing at the northern distribution limit.

The treeline site had significantly higher FA than the valley or the forest-limit site (Fig. 4). A higher amount of FA was also found in leaves in the middle position (Fig. 5) and in the west direction (Fig.6), although these values were not significant. Very little variation was found between the outer and inner crown leaves (Fig. 7).

5. DISCUSSION

Since plant growth is by accretion, and plants exhibit a relativity fixed orientation, slight differences in the environment on one side can become magnified over time (Freeman et al. 1993). Leaves in different parts of the crown of large plants experience different environments, and it follows that leaves on different parts of a plant may vary in developmental stability (Cowart & Graham 1999). In addition, the inherent plasticity that is a characteristic of plants can cause asymmetry that has little to do with developmental noise (Palmer 1996). For example, it is normal for trees to develop sun and shade leaves which, although genetically identical, can vary widely in their phenotype (Freeman et al. 1993). Thus, it is important in studies of fluctuating asymmetry (FA) in plants to ensure that such microsite variation is not incorporated into the variance component attributed to developmental stability (Freeman et al. 1993). If leaves are not selected carefully from different parts of a plant, then differences among individual plants may reflect sampling bias caused by within-plant variations in asymmetry (Cowart & Graham 1999).

Within plant variations in leaf FA have previously been found in a number of different species. Both tobacco (Paxman 1956; Sakai & Shimamoto 1965) and the herb Clarkia (Sherry & Lord 1996) have been shown to vary in FA values depending on the height of the node within the plant from which the leaf sample was collected. Leaf FA variation within trees has been studied in teak (Bagchi et al. 1989) and fig (Cowart & Graham 1999). In both cases, it was found that leaf FA varied with regard to position within the crown of the tree.

Although no research has previously been done on within tree variation of leaf FA in mountain birch, differences in leaf tissue composition and leaf morphology have been reported (Thórsson et al. 2007). Suomela & Ayres (1994) found a high degree of variation in water content, specific weight, toughness, and nitrogen content in mountain birch leaves; and for each of the traits measured, the within-tree variation was greater than the among-

tree variation. Within-tree leaf variation has also been shown in many studies on herbivore preferences for mountain birch foliage (Haukioja & Hanhimäki 1985; Ayres & Maclean 1987; Ayres et al. 1987; Karlsson & Nordell 1988; Haukioja et al. 1990; Senn et al. 1992; Suomela et al. 1995; Elamo et al. 1999). It is clear that environmental heterogeneity represents an extrinsic source of within-tree variation in mountain birch (Suomela & Ayres 1994).

In previous studies dealing with FA in mountain birch, leaves have either been collected haphazardly from random locations in the crown of the tree (Kozlov et al 1996; Wilsey et al. 1998; Martel et al 1999; Eränen et al. 2009), or else selected from an arbitrary location (e.g. second leaf from the base) (Valkama & Kozlov 2001; Kozlov 2003; Hagen et al. 2008). No study previously has examined whether variation for FA exists within the crown of the mountain birch.

This study did not find any variation in leaf FA at different locations within the tree crown. Height, direction, or proximity to the stem does not seem to affect leaf FA in mountain birch at the northern tree limit. There was a slightly higher amount of FA in the leaves at the middle height position and in the western direction, but these differences were not significant.

It could also be noted that previous studies of FA in mountain have used methods that involve great assumptions as to the consistency of leaves within a tree. Some studies have had sample sizes as small as two (Eränen et al. 2009) or three (Wilsey & Saloniemi 1999) leaves per tree, and none of the previous studies sampled more than ten leaves per tree. Some studies collected leaves from a combination of long and short shoots (Kozlov et al 1996; Rautio et al. 2002), which means that the leaves developed during different periods of growth (Kozlowski and Clausen 1966). I am also not aware of any other study that has used digital measurements instead of a handheld ruler for the right (*R*) and left (*L*) leaf width values. In addition to the ability to enlarge a digital image of a leaf, this technology also allows error check for directional bias in measurement, which I do not believe has ever been done in a FA analysis before.

It is possible that within tree FA variation in birch may be more pronounced in trees with more uniform crown formation. Many of the trees in this study, especially at the treeline, did not have very well defined crowns. Branching was sporadic and often sparse. With such a small range of possible leaf positions, all of the leaves within the tree were probably exposed to similar environmental factors. This may not have induced enough location specific stress influences to create variance in FA. In trees which lacked a well-defined crown, there was also very little shelter provided by outer leaves to reduce the stress on inner leaves, as was found in the study with fig trees (Cowart & Graham 1999). Most of the trees also had many ramets, and Suomela & Ayrres (1994) found variations in multiple leaf characteristics among ramets within mountain birch trees. It is possible that leaf FA could also vary among ramets within a tree. Further research could be done to see if variation in ramets affects FA in birch trees.

When comparing FA between birch growing at different elevation belts, this study found the treeline site had significantly higher FA than either the forest-limit or the valley site. This is consistent with previous studies (Wilsey et al. 1998; Hagen et al. 2008), which also found that leaf FA increased with elevation in mountain birch. The present study did not find a continuous increase in FA with elevation however, as the valley site was not significantly different from the forest-limit site.

It is possible that the valley site, although lower in elevation, was still a relatively high stress environment. The composition of the forest was similar at both the valley and the forest-limit site, and trees were relatively the same size and at the same density. The slight variation in elevation may not have been enough to cause a significant difference in FA values. If the valley site had been located in a more protected, lower elevation area, it is possible that a more clinal FA pattern would have emerged. However, this study was only attempting to determine if a relationship exists between leaf location and FA within the crown of mountain, and not comparing the possible effects of local environments.

6. CONCLUSION

The treeline site had significantly higher fluctuating asymmetry (FA) than either the forest-limit or the valley site. However, height, direction, or position within the crown had no effect on leaf FA at any of the elevational levels. There was no variation in leaf FA with respect to location within the crown of an individual tree. Therefore, for future studies of FA in mountain birch, it does not seem to matter where the leaves are collected from within the tree.

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APPENDIX

Fig. 8. Examples of typical birch trees (*Betula pubescens* spp. *czerepanovii*) from each elevation zone location: A) Valley site, B) Forest-limit site, C) Treeline site. Abisko, Sweden. August, 2010.

Fig. 9. Transition zone from forest-limit to treeline. Southeast slope of Mt Slåttatjåkka, Abisko, Sweden. August, 2010.

Fig. 10. Sample of birch (*B. pubescens* spp. *czerepanovii*) leaves collected from the Valley site. Abisko, Sweden. August, 2010.

Table 2. Raw data of left and right leaf width

Site	Height	Direction	Position	Left (cm)	Right (cm)
Forest-limit	Bottom	East	Inner	1.62	1.28
Forest-limit	Bottom	East	Inner	1.41	1.33
Forest-limit	Bottom	East	Inner	1.43	1.43
Forest-limit	Bottom	East	Inner	1.68	1.89
Forest-limit	Bottom	East	Inner	1.68	1.52
Forest-limit	Bottom	East	Inner	1.61	1.61
Forest-limit	Bottom	East	Inner	1.68	2.12
Forest-limit	Bottom	East	Inner	1.25	1.47
Forest-limit	Bottom	East	Inner	1.77	1.56
Forest-limit	Bottom	East	Inner	1.07	1.17
Forest-limit	Bottom	East	Outer	2.11	1.95
Forest-limit	Bottom	East	Outer	1.20	1.17
Forest-limit	Bottom	East	Outer	1.47	1.56
Forest-limit	Bottom	East	Outer	1.79	1.75
Forest-limit	Bottom	East	Outer	1.77	1.70
Forest-limit	Bottom	East	Outer	1.85	1.66
Forest-limit	Bottom	East	Outer	2.05	2.19
Forest-limit	Bottom	East	Outer	1.44	1.27
Forest-limit	Bottom	East	Outer	2.05	2.09
Forest-limit	Bottom	East	Outer	1.65	1.72
Forest-limit	Bottom	North	Inner	1.72	1.74
Forest-limit	Bottom	North	Inner	1.58	1.55
Forest-limit	Bottom	North	Inner	1.57	1.50
Forest-limit	Bottom	North	Inner	1.69	1.66
Forest-limit	Bottom	North	Inner	1.48	1.35
Forest-limit	Bottom	North	Inner	2.01	1.80
Forest-limit	Bottom	North	Inner	1.45	1.29
Forest-limit	Bottom	North	Inner	1.28	1.05
Forest-limit	Bottom	North	Inner	1.81	1.65
Forest-limit	Bottom	North	Inner	1.62	1.37
Forest-limit	Bottom	North	Outer	1.61	1.58
Forest-limit	Bottom	North	Outer	1.56	1.54
Forest-limit	Bottom	North	Outer	1.86	1.60
Forest-limit	Bottom	North	Outer	1.90	2.27
Forest-limit	Bottom	North	Outer	1.85	1.73
Forest-limit	Bottom	North	Outer	2.18	1.92

Forest-limit	Bottom	North	Outer	1.33	1.63
Forest-limit	Bottom	North	Outer	1.72	1.56
Forest-limit	Bottom	North	Outer	2.05	1.91
Forest-limit	Bottom	North	Outer	1.63	1.76
Forest-limit	Bottom	South	Inner	1.82	1.62
Forest-limit	Bottom	South	Inner	1.29	1.30
Forest-limit	Bottom	South	Inner	1.56	1.80
Forest-limit	Bottom	South	Inner	1.26	1.42
Forest-limit	Bottom	South	Inner	1.22	1.10
Forest-limit	Bottom	South	Inner	1.96	2.06
Forest-limit	Bottom	South	Inner	1.52	1.48
Forest-limit	Bottom	South	Inner	1.58	1.50
Forest-limit	Bottom	South	Inner	1.54	1.70
Forest-limit	Bottom	South	Inner	1.37	1.34
Forest-limit	Bottom	South	Outer	1.76	1.87
Forest-limit	Bottom	South	Outer	0.86	0.84
Forest-limit	Bottom	South	Outer	1.69	1.51
Forest-limit	Bottom	South	Outer	2.05	1.75
Forest-limit	Bottom	South	Outer	1.43	1.33
Forest-limit	Bottom	South	Outer	1.89	1.97
Forest-limit	Bottom	South	Outer	1.42	1.79
Forest-limit	Bottom	South	Outer	1.42	1.46
Forest-limit	Bottom	South	Outer	1.66	1.85
Forest-limit	Bottom	South	Outer	1.63	1.64
Forest-limit	Bottom	West	Inner	1.76	1.65
Forest-limit	Bottom	West	Inner	1.15	1.06
Forest-limit	Bottom	West	Inner	1.31	1.45
Forest-limit	Bottom	West	Inner	1.79	1.78
Forest-limit	Bottom	West	Inner	0.91	1.28
Forest-limit	Bottom	West	Inner	1.65	1.33
Forest-limit	Bottom	West	Inner	2.13	2.05
Forest-limit	Bottom	West	Inner	1.37	1.27
Forest-limit	Bottom	West	Inner	1.14	1.15
Forest-limit	Bottom	West	Inner	1.93	1.78
Forest-limit	Bottom	West	Outer	1.50	1.60
Forest-limit	Bottom	West	Outer	1.14	0.83
Forest-limit	Bottom	West	Outer	2.18	2.26
Forest-limit	Bottom	West	Outer	1.09	1.14
Forest-limit	Bottom	West	Outer	1.55	1.60

Forest-limit	Bottom	West	Outer	1.50	1.33
Forest-limit	Bottom	West	Outer	1.46	1.53
Forest-limit	Bottom	West	Outer	1.12	1.09
Forest-limit	Bottom	West	Outer	1.83	1.83
Forest-limit	Bottom	West	Outer	1.13	1.06
Forest-limit	Middle	East	Inner	1.52	1.55
Forest-limit	Middle	East	Inner	1.19	1.13
Forest-limit	Middle	East	Inner	1.58	1.61
Forest-limit	Middle	East	Inner	2.11	2.12
Forest-limit	Middle	East	Inner	2.04	1.92
Forest-limit	Middle	East	Inner	1.91	2.02
Forest-limit	Middle	East	Inner	1.69	1.49
Forest-limit	Middle	East	Inner	1.35	1.25
Forest-limit	Middle	East	Inner	1.96	1.93
Forest-limit	Middle	East	Inner	1.74	1.87
Forest-limit	Middle	East	Outer	1.87	2.05
Forest-limit	Middle	East	Outer	1.04	1.22
Forest-limit	Middle	East	Outer	1.25	1.18
Forest-limit	Middle	East	Outer	1.67	1.72
Forest-limit	Middle	East	Outer	1.43	1.43
Forest-limit	Middle	East	Outer	1.72	1.87
Forest-limit	Middle	East	Outer	1.40	1.35
Forest-limit	Middle	East	Outer	1.43	1.69
Forest-limit	Middle	East	Outer	1.17	1.11
Forest-limit	Middle	East	Outer	1.06	1.09
Forest-limit	Middle	North	Inner	1.66	1.64
Forest-limit	Middle	North	Inner	1.39	1.39
Forest-limit	Middle	North	Inner	0.97	0.82
Forest-limit	Middle	North	Inner	1.27	1.45
Forest-limit	Middle	North	Inner	1.38	1.47
Forest-limit	Middle	North	Inner	1.43	1.36
Forest-limit	Middle	North	Inner	1.38	1.33
Forest-limit	Middle	North	Inner	1.15	1.38
Forest-limit	Middle	North	Inner	1.64	1.58
Forest-limit	Middle	North	Inner	1.08	1.08
Forest-limit	Middle	North	Outer	2.27	2.30
Forest-limit	Middle	North	Outer	1.31	1.61
Forest-limit	Middle	North	Outer	1.35	1.55
Forest-limit	Middle	North	Outer	1.96	1.91

Forest-limit	Middle	North	Outer	1.22	1.55
Forest-limit	Middle	North	Outer	2.37	2.12
Forest-limit	Middle	North	Outer	1.18	1.13
Forest-limit	Middle	North	Outer	0.78	0.73
Forest-limit	Middle	North	Outer	1.19	1.04
Forest-limit	Middle	North	Outer	1.62	1.43
Forest-limit	Middle	South	Inner	2.24	1.92
Forest-limit	Middle	South	Inner	1.47	1.54
Forest-limit	Middle	South	Inner	1.78	1.84
Forest-limit	Middle	South	Inner	2.06	1.73
Forest-limit	Middle	South	Inner	1.07	1.01
Forest-limit	Middle	South	Inner	2.02	1.88
Forest-limit	Middle	South	Inner	1.47	1.74
Forest-limit	Middle	South	Inner	1.64	1.45
Forest-limit	Middle	South	Inner	1.40	1.41
Forest-limit	Middle	South	Inner	1.67	1.45
Forest-limit	Middle	South	Outer	1.95	2.02
Forest-limit	Middle	South	Outer	1.04	1.33
Forest-limit	Middle	South	Outer	1.20	1.26
Forest-limit	Middle	South	Outer	1.55	1.44
Forest-limit	Middle	South	Outer	1.30	1.36
Forest-limit	Middle	South	Outer	1.17	1.24
Forest-limit	Middle	South	Outer	1.16	1.33
Forest-limit	Middle	South	Outer	1.37	1.22
Forest-limit	Middle	South	Outer	1.42	1.37
Forest-limit	Middle	South	Outer	1.23	1.36
Forest-limit	Middle	West	Inner	1.20	1.65
Forest-limit	Middle	West	Inner	1.41	1.57
Forest-limit	Middle	West	Inner	1.50	1.71
Forest-limit	Middle	West	Inner	1.56	1.35
Forest-limit	Middle	West	Inner	1.73	1.56
Forest-limit	Middle	West	Inner	1.26	1.54
Forest-limit	Middle	West	Inner	1.81	1.94
Forest-limit	Middle	West	Inner	1.37	1.39
Forest-limit	Middle	West	Inner	1.24	1.51
Forest-limit	Middle	West	Inner	1.85	1.67
Forest-limit	Middle	West	Outer	2.05	1.72
Forest-limit	Middle	West	Outer	1.08	0.90
Forest-limit	Middle	West	Outer	1.31	1.40

Forest-limit	Middle	West	Outer	1.81	1.70
Forest-limit	Middle	West	Outer	1.29	0.98
Forest-limit	Middle	West	Outer	1.26	1.08
Forest-limit	Middle	West	Outer	1.26	1.35
Forest-limit	Middle	West	Outer	1.28	1.31
Forest-limit	Middle	West	Outer	1.21	1.12
Forest-limit	Middle	West	Outer	1.58	1.77
Forest-limit	Top	East	Inner	1.54	1.38
Forest-limit	Top	East	Inner	1.68	1.75
Forest-limit	Top	East	Inner	1.75	1.73
Forest-limit	Top	East	Inner	1.98	1.75
Forest-limit	Top	East	Inner	1.64	1.43
Forest-limit	Top	East	Inner	1.73	1.77
Forest-limit	Top	East	Inner	1.46	1.43
Forest-limit	Top	East	Inner	1.43	1.41
Forest-limit	Top	East	Inner	1.33	1.29
Forest-limit	Top	East	Inner	1.64	1.62
Forest-limit	Top	East	Outer	1.33	1.38
Forest-limit	Top	East	Outer	0.99	0.84
Forest-limit	Top	East	Outer	1.13	1.38
Forest-limit	Top	East	Outer	1.97	1.75
Forest-limit	Top	East	Outer	1.38	1.35
Forest-limit	Top	East	Outer	1.00	1.11
Forest-limit	Top	East	Outer	1.47	1.38
Forest-limit	Top	East	Outer	1.13	1.07
Forest-limit	Top	East	Outer	1.41	1.37
Forest-limit	Top	East	Outer	1.49	1.48
Forest-limit	Top	North	Inner	1.73	1.71
Forest-limit	Top	North	Inner	1.18	1.06
Forest-limit	Top	North	Inner	1.53	1.52
Forest-limit	Top	North	Inner	2.23	2.00
Forest-limit	Top	North	Inner	0.77	0.93
Forest-limit	Top	North	Inner	1.58	1.73
Forest-limit	Top	North	Inner	1.28	1.21
Forest-limit	Top	North	Inner	1.64	1.53
Forest-limit	Top	North	Inner	1.70	1.35
Forest-limit	Top	North	Inner	1.81	1.79
Forest-limit	Top	North	Outer	1.14	1.14
Forest-limit	Top	North	Outer	1.50	1.47

Forest-limit	Top	North	Outer	1.34	1.30
Forest-limit	Top	North	Outer	1.95	1.93
Forest-limit	Top	North	Outer	1.24	1.28
Forest-limit	Top	North	Outer	1.35	1.39
Forest-limit	Top	North	Outer	1.13	1.01
Forest-limit	Top	North	Outer	1.57	1.43
Forest-limit	Top	North	Outer	1.24	1.26
Forest-limit	Top	North	Outer	1.25	1.26
Forest-limit	Top	South	Inner	1.51	1.50
Forest-limit	Top	South	Inner	1.48	1.57
Forest-limit	Top	South	Inner	1.56	1.53
Forest-limit	Top	South	Inner	2.08	2.19
Forest-limit	Top	South	Inner	1.70	1.51
Forest-limit	Top	South	Inner	1.83	1.45
Forest-limit	Top	South	Inner	0.99	1.21
Forest-limit	Top	South	Inner	1.35	1.27
Forest-limit	Top	South	Inner	1.55	1.42
Forest-limit	Top	South	Inner	1.41	1.50
Forest-limit	Top	South	Outer	1.42	1.34
Forest-limit	Top	South	Outer	1.32	1.18
Forest-limit	Top	South	Outer	1.22	1.20
Forest-limit	Top	South	Outer	1.89	2.15
Forest-limit	Top	South	Outer	1.53	1.55
Forest-limit	Top	South	Outer	1.45	1.52
Forest-limit	Top	South	Outer	1.36	1.18
Forest-limit	Top	South	Outer	1.38	1.40
Forest-limit	Top	South	Outer	1.20	1.23
Forest-limit	Top	South	Outer	1.48	1.50
Forest-limit	Top	West	Inner	1.26	1.34
Forest-limit	Top	West	Inner	1.28	1.16
Forest-limit	Top	West	Inner	1.65	1.61
Forest-limit	Top	West	Inner	1.80	1.54
Forest-limit	Top	West	Inner	1.63	1.63
Forest-limit	Top	West	Inner	1.42	1.54
Forest-limit	Top	West	Inner	1.07	0.92
Forest-limit	Top	West	Inner	1.40	1.37
Forest-limit	Top	West	Inner	1.77	1.96
Forest-limit	Top	West	Inner	1.40	1.49
Forest-limit	Top	West	Outer	1.44	1.38

Forest-limit	Top	West	Outer	1.22	1.16
Forest-limit	Top	West	Outer	1.50	1.59
Forest-limit	Top	West	Outer	1.74	2.08
Forest-limit	Top	West	Outer	1.47	1.39
Forest-limit	Top	West	Outer	2.05	1.82
Forest-limit	Top	West	Outer	1.37	1.51
Forest-limit	Top	West	Outer	0.81	0.94
Forest-limit	Top	West	Outer	1.17	1.36
Forest-limit	Top	West	Outer	0.89	1.13
Tree-line	Bottom	East	Inner	1.89	1.95
Tree-line	Bottom	East	Inner	1.15	1.14
Tree-line	Bottom	East	Inner	1.77	1.71
Tree-line	Bottom	East	Inner	1.47	1.34
Tree-line	Bottom	East	Inner	1.12	1.05
Tree-line	Bottom	East	Inner	1.07	0.94
Tree-line	Bottom	East	Inner	1.08	0.88
Tree-line	Bottom	East	Inner	1.29	1.26
Tree-line	Bottom	East	Inner	1.78	1.34
Tree-line	Bottom	East	Inner	1.23	1.17
Tree-line	Bottom	East	Outer	1.97	1.84
Tree-line	Bottom	East	Outer	0.85	1.02
Tree-line	Bottom	East	Outer	1.66	1.22
Tree-line	Bottom	East	Outer	1.98	1.98
Tree-line	Bottom	East	Outer	1.35	1.54
Tree-line	Bottom	East	Outer	1.35	1.65
Tree-line	Bottom	East	Outer	1.44	1.65
Tree-line	Bottom	East	Outer	1.52	1.44
Tree-line	Bottom	East	Outer	2.60	2.58
Tree-line	Bottom	East	Outer	0.90	1.02
Tree-line	Bottom	North	Inner	1.30	1.60
Tree-line	Bottom	North	Inner	1.28	1.23
Tree-line	Bottom	North	Inner	1.34	1.41
Tree-line	Bottom	North	Inner	1.32	1.79
Tree-line	Bottom	North	Inner	1.21	1.14
Tree-line	Bottom	North	Inner	1.55	1.52
Tree-line	Bottom	North	Inner	1.55	1.55
Tree-line	Bottom	North	Inner	1.28	1.36
Tree-line	Bottom	North	Inner	1.71	1.61
Tree-line	Bottom	North	Inner	1.22	1.25

Tree-line	Bottom	North	Outer	2.34	2.32
Tree-line	Bottom	North	Outer	1.66	1.65
Tree-line	Bottom	North	Outer	1.81	1.81
Tree-line	Bottom	North	Outer	1.87	1.93
Tree-line	Bottom	North	Outer	1.19	1.19
Tree-line	Bottom	North	Outer	1.81	1.40
Tree-line	Bottom	North	Outer	1.50	1.42
Tree-line	Bottom	North	Outer	1.17	1.21
Tree-line	Bottom	North	Outer	1.76	1.36
Tree-line	Bottom	North	Outer	1.61	1.66
Tree-line	Bottom	South	Inner	1.95	1.80
Tree-line	Bottom	South	Inner	1.34	1.35
Tree-line	Bottom	South	Inner	1.32	1.32
Tree-line	Bottom	South	Inner	0.93	1.06
Tree-line	Bottom	South	Inner	1.85	1.41
Tree-line	Bottom	South	Inner	1.48	1.47
Tree-line	Bottom	South	Inner	1.49	1.51
Tree-line	Bottom	South	Inner	1.23	0.99
Tree-line	Bottom	South	Inner	0.89	0.87
Tree-line	Bottom	South	Inner	1.36	1.31
Tree-line	Bottom	South	Outer	1.78	1.84
Tree-line	Bottom	South	Outer	1.26	1.10
Tree-line	Bottom	South	Outer	1.75	1.58
Tree-line	Bottom	South	Outer	2.04	2.12
Tree-line	Bottom	South	Outer	1.35	1.20
Tree-line	Bottom	South	Outer	1.52	1.77
Tree-line	Bottom	South	Outer	1.45	1.71
Tree-line	Bottom	South	Outer	1.61	1.47
Tree-line	Bottom	South	Outer	1.50	1.68
Tree-line	Bottom	South	Outer	1.27	1.19
Tree-line	Bottom	West	Inner	1.33	1.06
Tree-line	Bottom	West	Inner	1.78	1.67
Tree-line	Bottom	West	Inner	1.04	1.07
Tree-line	Bottom	West	Inner	0.88	1.13
Tree-line	Bottom	West	Inner	1.45	0.99
Tree-line	Bottom	West	Inner	2.17	1.94
Tree-line	Bottom	West	Inner	2.17	1.91
Tree-line	Bottom	West	Inner	1.43	1.36
Tree-line	Bottom	West	Inner	2.15	1.99

Tree-line	Bottom	West	Inner	1.75	1.69
Tree-line	Bottom	West	Outer	1.60	1.79
Tree-line	Bottom	West	Outer	1.18	1.13
Tree-line	Bottom	West	Outer	1.34	1.05
Tree-line	Bottom	West	Outer	2.20	2.19
Tree-line	Bottom	West	Outer	1.45	1.56
Tree-line	Bottom	West	Outer	1.34	1.54
Tree-line	Bottom	West	Outer	1.33	1.57
Tree-line	Bottom	West	Outer	1.49	1.35
Tree-line	Bottom	West	Outer	1.57	1.71
Tree-line	Bottom	West	Outer	1.21	1.14
Tree-line	Middle	East	Inner	1.94	2.07
Tree-line	Middle	East	Inner	1.65	1.56
Tree-line	Middle	East	Inner	1.04	1.30
Tree-line	Middle	East	Inner	1.29	1.39
Tree-line	Middle	East	Inner	1.21	1.10
Tree-line	Middle	East	Inner	1.68	1.68
Tree-line	Middle	East	Inner	1.59	1.61
Tree-line	Middle	East	Inner	1.34	1.38
Tree-line	Middle	East	Inner	0.95	1.40
Tree-line	Middle	East	Inner	1.41	1.68
Tree-line	Middle	East	Outer	2.20	2.47
Tree-line	Middle	East	Outer	0.97	0.95
Tree-line	Middle	East	Outer	1.13	1.39
Tree-line	Middle	East	Outer	1.27	1.18
Tree-line	Middle	East	Outer	1.36	1.44
Tree-line	Middle	East	Outer	1.71	1.68
Tree-line	Middle	East	Outer	1.41	1.70
Tree-line	Middle	East	Outer	1.31	1.33
Tree-line	Middle	East	Outer	1.00	1.02
Tree-line	Middle	East	Outer	1.16	1.12
Tree-line	Middle	North	Inner	2.19	2.16
Tree-line	Middle	North	Inner	1.52	1.52
Tree-line	Middle	North	Inner	1.31	1.35
Tree-line	Middle	North	Inner	2.25	2.27
Tree-line	Middle	North	Inner	1.41	1.41
Tree-line	Middle	North	Inner	1.72	1.58
Tree-line	Middle	North	Inner	1.74	1.54
Tree-line	Middle	North	Inner	1.42	1.22

Tree-line	Middle	North	Inner	1.96	1.96
Tree-line	Middle	North	Inner	1.47	1.45
Tree-line	Middle	North	Outer	1.75	1.81
Tree-line	Middle	North	Outer	1.20	1.05
Tree-line	Middle	North	Outer	1.31	1.54
Tree-line	Middle	North	Outer	2.27	2.25
Tree-line	Middle	North	Outer	1.57	1.27
Tree-line	Middle	North	Outer	1.87	2.01
Tree-line	Middle	North	Outer	1.91	2.01
Tree-line	Middle	North	Outer	1.50	1.26
Tree-line	Middle	North	Outer	1.60	1.84
Tree-line	Middle	North	Outer	1.18	1.11
Tree-line	Middle	South	Inner	1.59	1.63
Tree-line	Middle	South	Inner	1.22	1.14
Tree-line	Middle	South	Inner	1.44	1.23
Tree-line	Middle	South	Inner	0.90	0.99
Tree-line	Middle	South	Inner	0.91	0.99
Tree-line	Middle	South	Inner	1.24	1.19
Tree-line	Middle	South	Inner	1.82	1.67
Tree-line	Middle	South	Inner	1.11	1.09
Tree-line	Middle	South	Inner	1.73	1.79
Tree-line	Middle	South	Inner	1.30	1.13
Tree-line	Middle	South	Outer	1.84	1.65
Tree-line	Middle	South	Outer	0.77	0.76
Tree-line	Middle	South	Outer	1.67	1.59
Tree-line	Middle	South	Outer	1.84	1.88
Tree-line	Middle	South	Outer	1.54	1.25
Tree-line	Middle	South	Outer	1.70	1.33
Tree-line	Middle	South	Outer	1.34	1.61
Tree-line	Middle	South	Outer	1.28	1.36
Tree-line	Middle	South	Outer	1.64	1.72
Tree-line	Middle	South	Outer	0.86	0.86
Tree-line	Middle	West	Inner	1.86	1.69
Tree-line	Middle	West	Inner	1.72	1.71
Tree-line	Middle	West	Inner	1.56	1.59
Tree-line	Middle	West	Inner	1.56	1.39
Tree-line	Middle	West	Inner	1.39	1.29
Tree-line	Middle	West	Inner	1.88	1.40
Tree-line	Middle	West	Inner	1.87	1.39

Tree-line	Middle	West	Inner	1.39	1.29
Tree-line	Middle	West	Inner	1.41	1.44
Tree-line	Middle	West	Inner	1.66	1.74
Tree-line	Middle	West	Outer	1.41	1.41
Tree-line	Middle	West	Outer	0.87	0.87
Tree-line	Middle	West	Outer	1.61	1.55
Tree-line	Middle	West	Outer	2.44	2.12
Tree-line	Middle	West	Outer	1.34	1.43
Tree-line	Middle	West	Outer	1.95	1.49
Tree-line	Middle	West	Outer	1.88	1.43
Tree-line	Middle	West	Outer	1.53	1.33
Tree-line	Middle	West	Outer	1.68	1.62
Tree-line	Middle	West	Outer	0.86	0.87
Tree-line	Top	East	Inner	1.72	1.68
Tree-line	Top	East	Inner	1.30	1.42
Tree-line	Top	East	Inner	1.24	1.34
Tree-line	Top	East	Inner	1.52	1.35
Tree-line	Top	East	Inner	1.50	1.25
Tree-line	Top	East	Inner	1.81	1.67
Tree-line	Top	East	Inner	1.94	1.91
Tree-line	Top	East	Inner	1.07	1.25
Tree-line	Top	East	Inner	2.10	2.10
Tree-line	Top	East	Inner	1.38	1.10
Tree-line	Top	East	Outer	1.30	1.17
Tree-line	Top	East	Outer	1.11	1.04
Tree-line	Top	East	Outer	1.35	1.34
Tree-line	Top	East	Outer	1.31	1.14
Tree-line	Top	East	Outer	0.92	0.92
Tree-line	Top	East	Outer	1.20	0.91
Tree-line	Top	East	Outer	1.68	1.70
Tree-line	Top	East	Outer	1.24	1.35
Tree-line	Top	East	Outer	1.24	1.19
Tree-line	Top	East	Outer	1.10	1.13
Tree-line	Top	North	Inner	1.77	1.72
Tree-line	Top	North	Inner	1.06	1.09
Tree-line	Top	North	Inner	0.89	1.01
Tree-line	Top	North	Inner	1.99	1.85
Tree-line	Top	North	Inner	1.04	0.98
Tree-line	Top	North	Inner	1.05	1.24

Tree-line	Top	North	Inner	1.64	1.72
Tree-line	Top	North	Inner	1.15	1.11
Tree-line	Top	North	Inner	1.07	1.17
Tree-line	Top	North	Inner	0.95	0.84
Tree-line	Top	North	Outer	1.52	1.45
Tree-line	Top	North	Outer	1.34	1.32
Tree-line	Top	North	Outer	1.11	1.12
Tree-line	Top	North	Outer	1.62	1.34
Tree-line	Top	North	Outer	0.96	0.91
Tree-line	Top	North	Outer	1.20	1.17
Tree-line	Top	North	Outer	1.67	1.29
Tree-line	Top	North	Outer	1.12	1.05
Tree-line	Top	North	Outer	1.37	1.40
Tree-line	Top	North	Outer	1.04	0.88
Tree-line	Top	South	Inner	1.75	1.68
Tree-line	Top	South	Inner	1.46	1.52
Tree-line	Top	South	Inner	1.16	1.01
Tree-line	Top	South	Inner	1.86	2.04
Tree-line	Top	South	Inner	1.17	1.45
Tree-line	Top	South	Inner	1.50	1.31
Tree-line	Top	South	Inner	1.42	1.35
Tree-line	Top	South	Inner	1.37	1.39
Tree-line	Top	South	Inner	1.76	1.65
Tree-line	Top	South	Inner	1.75	1.40
Tree-line	Top	South	Outer	1.69	1.48
Tree-line	Top	South	Outer	1.11	1.07
Tree-line	Top	South	Outer	1.48	1.26
Tree-line	Top	South	Outer	1.51	1.30
Tree-line	Top	South	Outer	1.15	1.03
Tree-line	Top	South	Outer	1.26	1.25
Tree-line	Top	South	Outer	1.68	1.35
Tree-line	Top	South	Outer	1.09	0.97
Tree-line	Top	South	Outer	1.26	1.16
Tree-line	Top	South	Outer	1.21	1.15
Tree-line	Top	West	Inner	1.68	1.66
Tree-line	Top	West	Inner	0.94	0.91
Tree-line	Top	West	Inner	0.92	0.93
Tree-line	Top	West	Inner	1.64	1.51
Tree-line	Top	West	Inner	1.14	1.00

Tree-line	Top	West	Inner	1.44	1.40
Tree-line	Top	West	Inner	1.05	1.16
Tree-line	Top	West	Inner	1.34	1.18
Tree-line	Top	West	Inner	1.79	1.59
Tree-line	Top	West	Inner	0.99	1.11
Tree-line	Top	West	Outer	1.95	1.77
Tree-line	Top	West	Outer	1.18	1.13
Tree-line	Top	West	Outer	0.78	0.97
Tree-line	Top	West	Outer	2.09	2.09
Tree-line	Top	West	Outer	1.40	1.44
Tree-line	Top	West	Outer	1.30	1.28
Tree-line	Top	West	Outer	1.69	1.29
Tree-line	Top	West	Outer	1.35	1.26
Tree-line	Top	West	Outer	1.75	1.44
Tree-line	Top	West	Outer	0.89	0.85
Valley	Bottom	East	Inner	1.17	1.37
Valley	Bottom	East	Inner	1.34	1.25
Valley	Bottom	East	Inner	0.96	1.21
Valley	Bottom	East	Inner	1.50	1.66
Valley	Bottom	East	Inner	1.49	1.36
Valley	Bottom	East	Inner	1.61	1.64
Valley	Bottom	East	Inner	1.54	1.59
Valley	Bottom	East	Inner	1.59	1.42
Valley	Bottom	East	Inner	1.35	1.15
Valley	Bottom	East	Inner	1.79	2.13
Valley	Bottom	East	Outer	1.69	1.27
Valley	Bottom	East	Outer	1.31	1.40
Valley	Bottom	East	Outer	1.90	1.76
Valley	Bottom	East	Outer	1.63	1.61
Valley	Bottom	East	Outer	1.17	1.19
Valley	Bottom	East	Outer	1.66	1.64
Valley	Bottom	East	Outer	1.54	1.50
Valley	Bottom	East	Outer	1.37	1.40
Valley	Bottom	East	Outer	1.07	1.18
Valley	Bottom	East	Outer	0.93	0.83
Valley	Bottom	North	Inner	1.81	1.70
Valley	Bottom	North	Inner	1.26	1.33
Valley	Bottom	North	Inner	1.41	1.55
Valley	Bottom	North	Inner	1.56	1.85

Valley	Bottom	North	Inner	2.09	1.96
Valley	Bottom	North	Inner	1.36	1.20
Valley	Bottom	North	Inner	0.95	0.89
Valley	Bottom	North	Inner	1.53	1.49
Valley	Bottom	North	Inner	1.29	1.37
Valley	Bottom	North	Inner	1.86	1.79
Valley	Bottom	North	Outer	1.39	1.41
Valley	Bottom	North	Outer	1.18	1.18
Valley	Bottom	North	Outer	1.39	1.79
Valley	Bottom	North	Outer	1.51	1.71
Valley	Bottom	North	Outer	1.46	1.41
Valley	Bottom	North	Outer	1.75	1.77
Valley	Bottom	North	Outer	1.45	1.33
Valley	Bottom	North	Outer	1.47	1.39
Valley	Bottom	North	Outer	1.70	1.56
Valley	Bottom	North	Outer	0.83	0.67
Valley	Bottom	South	Inner	1.44	1.47
Valley	Bottom	South	Inner	1.78	1.92
Valley	Bottom	South	Inner	1.25	1.17
Valley	Bottom	South	Inner	1.42	1.45
Valley	Bottom	South	Inner	1.68	1.63
Valley	Bottom	South	Inner	1.56	1.67
Valley	Bottom	South	Inner	0.98	0.87
Valley	Bottom	South	Inner	1.35	1.00
Valley	Bottom	South	Inner	1.67	1.43
Valley	Bottom	South	Inner	2.23	1.84
Valley	Bottom	South	Outer	0.96	1.38
Valley	Bottom	South	Outer	1.24	1.26
Valley	Bottom	South	Outer	1.56	1.65
Valley	Bottom	South	Outer	1.92	1.67
Valley	Bottom	South	Outer	1.57	1.30
Valley	Bottom	South	Outer	1.70	1.51
Valley	Bottom	South	Outer	1.29	1.17
Valley	Bottom	South	Outer	1.29	1.19
Valley	Bottom	South	Outer	1.62	1.54
Valley	Bottom	South	Outer	1.50	1.31
Valley	Bottom	West	Inner	1.44	1.43
Valley	Bottom	West	Inner	1.22	1.21
Valley	Bottom	West	Inner	1.42	1.39

Valley	Bottom	West	Inner	1.26	1.21
Valley	Bottom	West	Inner	1.07	1.02
Valley	Bottom	West	Inner	1.52	1.41
Valley	Bottom	West	Inner	1.09	1.01
Valley	Bottom	West	Inner	1.45	1.56
Valley	Bottom	West	Inner	1.36	1.21
Valley	Bottom	West	Inner	1.39	1.43
Valley	Bottom	West	Outer	1.91	1.65
Valley	Bottom	West	Outer	1.44	1.51
Valley	Bottom	West	Outer	1.34	1.29
Valley	Bottom	West	Outer	1.68	1.79
Valley	Bottom	West	Outer	1.25	1.26
Valley	Bottom	West	Outer	1.08	1.08
Valley	Bottom	West	Outer	1.27	1.11
Valley	Bottom	West	Outer	1.09	1.14
Valley	Bottom	West	Outer	1.56	1.45
Valley	Bottom	West	Outer	0.98	1.01
Valley	Middle	East	Inner	1.95	1.68
Valley	Middle	East	Inner	1.25	1.06
Valley	Middle	East	Inner	1.85	1.70
Valley	Middle	East	Inner	1.45	1.71
Valley	Middle	East	Inner	1.83	1.80
Valley	Middle	East	Inner	1.04	1.10
Valley	Middle	East	Inner	1.36	1.33
Valley	Middle	East	Inner	1.05	1.19
Valley	Middle	East	Inner	1.56	1.54
Valley	Middle	East	Inner	1.80	1.68
Valley	Middle	East	Outer	1.45	1.22
Valley	Middle	East	Outer	1.31	1.31
Valley	Middle	East	Outer	1.94	1.96
Valley	Middle	East	Outer	1.35	1.41
Valley	Middle	East	Outer	0.83	0.86
Valley	Middle	East	Outer	1.40	1.33
Valley	Middle	East	Outer	1.27	1.20
Valley	Middle	East	Outer	1.21	1.33
Valley	Middle	East	Outer	1.51	1.55
Valley	Middle	East	Outer	1.47	1.46
Valley	Middle	North	Inner	2.04	1.96
Valley	Middle	North	Inner	1.55	1.46

Valley	Middle	North	Inner	1.67	1.61
Valley	Middle	North	Inner	1.64	1.50
Valley	Middle	North	Inner	1.71	1.70
Valley	Middle	North	Inner	1.57	1.55
Valley	Middle	North	Inner	0.92	0.91
Valley	Middle	North	Inner	1.29	1.31
Valley	Middle	North	Inner	1.24	1.09
Valley	Middle	North	Inner	1.21	1.16
Valley	Middle	North	Outer	1.23	1.20
Valley	Middle	North	Outer	1.39	1.21
Valley	Middle	North	Outer	1.55	1.51
Valley	Middle	North	Outer	1.59	1.69
Valley	Middle	North	Outer	1.30	1.15
Valley	Middle	North	Outer	1.41	1.47
Valley	Middle	North	Outer	1.38	1.37
Valley	Middle	North	Outer	1.45	1.51
Valley	Middle	North	Outer	1.54	1.58
Valley	Middle	North	Outer	1.27	1.25
Valley	Middle	South	Inner	1.78	1.58
Valley	Middle	South	Inner	1.37	1.23
Valley	Middle	South	Inner	1.36	1.40
Valley	Middle	South	Inner	1.99	2.03
Valley	Middle	South	Inner	1.37	1.31
Valley	Middle	South	Inner	1.67	1.68
Valley	Middle	South	Inner	1.26	1.17
Valley	Middle	South	Inner	1.51	1.40
Valley	Middle	South	Inner	1.50	1.34
Valley	Middle	South	Inner	1.71	1.48
Valley	Middle	South	Outer	1.46	1.71
Valley	Middle	South	Outer	1.83	1.78
Valley	Middle	South	Outer	1.80	1.70
Valley	Middle	South	Outer	1.53	1.57
Valley	Middle	South	Outer	1.08	1.12
Valley	Middle	South	Outer	1.99	1.92
Valley	Middle	South	Outer	1.56	1.23
Valley	Middle	South	Outer	1.38	1.30
Valley	Middle	South	Outer	1.23	1.35
Valley	Middle	South	Outer	1.63	1.60
Valley	Middle	West	Inner	1.88	1.82

Valley	Middle	West	Inner	1.44	1.72
Valley	Middle	West	Inner	1.19	1.19
Valley	Middle	West	Inner	1.90	1.86
Valley	Middle	West	Inner	1.38	1.27
Valley	Middle	West	Inner	1.66	1.81
Valley	Middle	West	Inner	1.21	1.13
Valley	Middle	West	Inner	1.66	1.80
Valley	Middle	West	Inner	1.04	1.32
Valley	Middle	West	Inner	1.12	1.09
Valley	Middle	West	Outer	1.31	1.31
Valley	Middle	West	Outer	1.33	1.08
Valley	Middle	West	Outer	1.60	1.49
Valley	Middle	West	Outer	1.61	1.69
Valley	Middle	West	Outer	1.40	1.34
Valley	Middle	West	Outer	1.30	1.17
Valley	Middle	West	Outer	1.40	1.29
Valley	Middle	West	Outer	1.27	1.33
Valley	Middle	West	Outer	1.54	1.44
Valley	Middle	West	Outer	1.31	1.34
Valley	Top	East	Inner	1.31	1.14
Valley	Top	East	Inner	1.41	1.43
Valley	Top	East	Inner	1.29	1.37
Valley	Top	East	Inner	1.34	1.53
Valley	Top	East	Inner	1.60	1.54
Valley	Top	East	Inner	1.31	1.07
Valley	Top	East	Inner	0.93	1.13
Valley	Top	East	Inner	1.78	1.46
Valley	Top	East	Inner	1.56	1.41
Valley	Top	East	Inner	1.75	1.76
Valley	Top	East	Outer	1.29	1.30
Valley	Top	East	Outer	1.35	1.31
Valley	Top	East	Outer	1.66	1.64
Valley	Top	East	Outer	1.28	1.45
Valley	Top	East	Outer	1.21	1.24
Valley	Top	East	Outer	1.48	1.57
Valley	Top	East	Outer	1.17	1.11
Valley	Top	East	Outer	1.50	1.43
Valley	Top	East	Outer	1.20	0.92
Valley	Top	East	Outer	1.55	1.59

Valley	Top	North	Inner	1.32	1.16
Valley	Top	North	Inner	1.37	1.43
Valley	Top	North	Inner	1.30	1.20
Valley	Top	North	Inner	1.10	1.20
Valley	Top	North	Inner	1.57	1.42
Valley	Top	North	Inner	1.51	1.34
Valley	Top	North	Inner	1.19	1.15
Valley	Top	North	Inner	1.27	1.26
Valley	Top	North	Inner	1.37	1.26
Valley	Top	North	Inner	1.77	1.52
Valley	Top	North	Outer	1.06	1.16
Valley	Top	North	Outer	0.98	1.03
Valley	Top	North	Outer	1.48	1.47
Valley	Top	North	Outer	1.61	1.36
Valley	Top	North	Outer	0.97	0.89
Valley	Top	North	Outer	1.29	1.43
Valley	Top	North	Outer	1.04	1.14
Valley	Top	North	Outer	0.96	1.12
Valley	Top	North	Outer	1.48	1.16
Valley	Top	North	Outer	1.38	1.50
Valley	Top	South	Inner	1.41	1.33
Valley	Top	South	Inner	1.13	1.14
Valley	Top	South	Inner	1.71	1.69
Valley	Top	South	Inner	1.45	1.30
Valley	Top	South	Inner	1.22	1.30
Valley	Top	South	Inner	1.33	1.41
Valley	Top	South	Inner	0.96	0.96
Valley	Top	South	Inner	1.02	1.08
Valley	Top	South	Inner	1.09	1.27
Valley	Top	South	Inner	1.17	1.10
Valley	Top	South	Outer	1.18	1.10
Valley	Top	South	Outer	1.21	1.32
Valley	Top	South	Outer	1.87	1.72
Valley	Top	South	Outer	1.57	1.64
Valley	Top	South	Outer	1.24	1.26
Valley	Top	South	Outer	1.56	1.49
Valley	Top	South	Outer	1.33	1.32
Valley	Top	South	Outer	1.14	1.10
Valley	Top	South	Outer	1.09	0.99

Valley	Top	South	Outer	1.31	1.36
Valley	Top	West	Inner	1.37	1.48
Valley	Top	West	Inner	1.13	1.21
Valley	Top	West	Inner	1.24	1.37
Valley	Top	West	Inner	1.07	1.19
Valley	Top	West	Inner	1.26	1.33
Valley	Top	West	Inner	1.03	1.24
Valley	Top	West	Inner	1.03	0.89
Valley	Top	West	Inner	1.23	1.25
Valley	Top	West	Inner	1.23	1.33
Valley	Top	West	Inner	1.52	1.46
Valley	Top	West	Outer	1.40	1.39
Valley	Top	West	Outer	1.54	1.32
Valley	Top	West	Outer	1.37	1.41
Valley	Top	West	Outer	1.39	1.31
Valley	Top	West	Outer	1.44	1.56
Valley	Top	West	Outer	1.52	1.60
Valley	Top	West	Outer	1.21	1.10
Valley	Top	West	Outer	0.95	0.99
Valley	Top	West	Outer	1.08	1.20
Valley	Top	West	Outer	1.75	1.71